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Population Structuring and Transmission Dynamics of a Laboratory Colony of Gromphadorholaelaps schaeferi: A Symbiotic Mite of the Madagascar Hissing Cockroach Gromphadorhina portentosa

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Population Structuring and Transmission Dynamics of a Laboratory Colony of *Gromphadorholaelaps schaeferi*: A Symbiotic Mite of the Madagascar Hissing Cockroach *Gromphadorhina portentosa*

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Abstract

Gromphadorholaelaps schaeferi is a symbiotic mite associated with the Madagascar hissing cockroach *Gromphdorhina portentosa*. The population structuring of *G. schaeferi* is described based on examination of 19,421 mites collected from 1,915 individuals of *G. portentosa* taken from a large laboratory colony. The mites exhibited an overall prevalence of 50.7% and mean intensity (±SE) of 20.0 (±0.6) with an infestation intensity range of 1-116, and relative abundance (±SE) of 10.1 (±0.4). Both prevalence and mean intensity of infestation exhibited a dramatic increase with increasing cockroach size/age. By the time cockroaches reach 40 mm the prevalence is nearly 100%. Mean intensity increases with cockroach length up to about 60 mm and then levels off at about 43 mites/cockroach. Overall, the mite distribution among cockroaches exhibited pronounced overdispersion with a variance to mean ratio of 30.1 and *k* value of 0.182101. Nevertheless, the distribution of mites on *G. portentosa* did not conform to expected values of the "classic" negative binomial distribution due to a greater number of moderate infestations than expected and a lower number of heavy infestations than expected.

Introduction

Because it is large, docile, and easy to breed and maintain in captivity, the Madagascar hissing cockroach *Gromphadorhina portentosa* is commonly kept in museums, zoos, nature centers, and classrooms. Individuals of *G. portentosa* are robust insects that may attain a length of up to 78 mm (Gurney 1959), making these among the largest of the cockroaches (Bell et al. 2007). Despite its popularity there is a relative paucity of knowledge on the basic biology of this organism in the laboratory and even less is known of its biology in nature. The scant information that has been published concerning the biology of natural populations of *G. portentosa* are anecdotal, highly speculative and may be summarized as follows: Marcillo (1993) stated that *G. portentosa* lives in large colonies among rotting logs and other plant materials in the jungles of Madagascar. Varadínova et al. (2010) stated that they inhabit dry forests and form small groups consisting of about 10 individuals. Yoder and Grojean (1997) stated that *G. portentosa* lives in dry litter on the floor of tropical rain forests and further speculated that in order to maximize water retention, they live huddled together in nests under rocks or bark in caves. Yoder et al. (2009) speculated that they form aggregations of several hundred individuals in leaf litter on the forest floor. Darmo and Ludwig (1995) stated that *G. portentosa* appears to play the ecological role of scavenger on or near rotten logs in savannah areas.

The life history of *G. portentosa* is nearly as poorly known as its biology in nature. The current published knowledge concerning its life history may be summarized as follows: Cockroaches are ovoviviparous, giving birth to approximately 20-40 young following a gestation period of 60-70 days (Yoder and Grojean 1997). The young reportedly huddle under the mother for several instars after birth (Roth and Willis, 1960). The life history includes 6 nymphal instars, persisting about one month each, and an adult and is completed in about 7 months (Yoder 1996). The life span is estimated to be 2 to 3 years (Darmo and Ludwig 1995).

Gromphadorholaelaps schaeferi, the only symbiotic mite known to be associated with *G. portentosa*, was originally described by Till (1969) from individuals found infesting laboratory colonies of *G. portentosa* at the University of Connecticut. These mites were first reported by Roth and Willis (1960) on individuals of *G. portentosa* presumably imported into the United States from Madagascar via Europe (Till 1969). Mites live on cockroaches aggregating on membranous areas of the thoracic sterna, at the base of the leg, and around the thoracic spiracles (Yoder and Barcelona 1995) where they are ptyalophagous,

feeding primarily on saliva of the cockroach and absorbing water vapor (Yoder 1996). Unmated female mites are parthenogenetic and give birth only to males (Yoder 1996). *Gromphadorholaelaps schaeferi* is larviparous lacking an egg and exhibiting four post-embryonic stages, larva, protonymph, deutonymph, and adult. Adult females give birth to a single larva. The larval instar persists for only four to eight hours. The protonymph and deutonymph stages persist about 4 and 20 days respectively (Yoder 1996). Yoder (1996) termed the ephemeral larval stage a 'shoot-through' larva and suggested that the highly reduced time spent in the larval instar is an adaptation to avoid predation by their mothers which exhibit larvacidal tendencies.

Schaefer and Peckham (1968) reported that young cockroaches are infested while huddling in a clutch under their mother. This constitutes vertical transmission, or transmission from parent to offspring. Likewise, Schaefer and Peckham (1968) noted that mites were rarely observed in the litter or on the food of the cockroaches. Schaefer and Peckham (1968) also indicated that mites "do not search far to find a host", and that when a newly dead cockroach was removed from the colony the mites would wander on it until they too died. However, Schaefer and Peckham (1968) pointed out that under normal circumstances, other living hosts would be near the body providing an avenue for horizontal transmission (i.e. transmission by other means than from parent to offspring). Based on these observations, Yoder (1996) suggested that *G. schaeferi* exhibits high host fidelity and concluded that parthenogenetic female mites use the cockroach for colony founding and that the larger numbers of mites on adult cockroaches represent independent populations started largely by the single female foundress, and are thus a result of vertical transmission.

Alternatively, if mites are found to exhibit a relatively high degree of vagility and low host fidelity, horizontal transmission may play an important role in transmission. It has been postulated that in nature, *Gromphadorhina portentosa* is a social insect (Nelson and Fraser, 1980) that forms aggregations of hundreds of individuals in the leaf litter on the rainforest floor (Yoder and Grojean 1997; Yoder et al. 2009). Such an environment would provide an excellent opportunity for frequent horizontal transmission of mites among cockroaches. The relative degree of vertical as opposed to horizontal transmission has profound implications in regard to population structuring of symbionts on their hosts. As pointed out by Whiteman and Parker (2004), populations of symbiotic organisms that are at least partially horizontally transmitted should be affected by host population density, whereas those that are more dependent on vertical transmission (parent-offspring) should be less affected by host population density.

No previous study has provided a comprehensive account of the population structuring of *G. schaeferi* from a large population of *G. portentosa.* Yoder (1996) reported the occurrence of mites on 25 adult female *G. portentosa* exhibiting a prevalence of 100%, mean intensity ($\pm$SE) of 20.0 ($\pm$0.5) and range of 14-24.

The purpose of this study was to more fully describe the population structuring of *G. schaeferi* on *G. portentosa* and to gain insight into the transmission dynamics of this mite, specifically to determine the extent to which horizontal transmission of *G. schaeferi* occurs among *G. portentosa* comprising a large colony of approximately 4,000 cockroaches.

Materials and Methods

Cockroaches were maintained in a large colony in a 151 l glass terrarium. The colony was essentially divided into two equivalent parts with each part being comprised of egg cartons stacked to a height of about 250 cm. Sterilized cypress bark was provided as bedding. The two halves of the colony were separated by the food and water containers. The temperature was maintained at about 27 ˚C using ceramic heaters and the colony was maintained at ambient relative humidity with a 12 hr/12 hr, light/dark photoperiod. Cockroaches were given water and food (Beneful® dogfood) *ad libitum*.

Description of Population Structuring of G. schaeferi

Over a six wk period, one half/side of the colony was dismantled and all cockroaches inhabiting that side of the colony were collected, measured, and mites were removed from cockroaches over 20 mm long with a camel hair paint brush and counted. Mites were brushed onto white paper and counted with the unaided eye. Subsequent to examination, cockroaches and mites were placed in a new terrarium. Sex of cockroaches ($\geq$ 50 mm long) was discriminated based on the presence of pronotal horns on male cockroaches and differences in subgenal plates as described by Delfosse (2004). Cockroaches $\leq$ 20 mm long were placed into a vial containing 95% ethanol for mite removal because these were too small to remove mites

by brushing. Contents of vials containing the small cockroaches were shaken, emptied into a gridded Petri dish, and examined for mites under a dissecting microscope.

The prevalence of infestation was determined by dividing the number of cockroaches sampled by the number infested with *G. schaeferi*. Mean intensity was determined by dividing the total number of mites collected by the number of infested cockroaches and relative abundance was determined by dividing the total number of mites collected by the total number of cockroaches examined, including both infested and uninfested individuals. Mean intensities between sexes and size classes of cockroaches were compared using Student's two-tailed t-tests. The overdispersion parameter *k* was calculated using Fisher's maximum likelihood technique (Bliss and Fisher 1953). The negative binomial distribution (Fisher 1941) was fit to the data and the goodness of fit was tested by comparison of observed and expected frequencies by Chi-square analysis as described by Bliss and Fisher (1953).

Investigation of Transmission Dynamics and Response to Light of G. schaeferi on G. portentosa

Mites were removed from 40 adult cockroaches, 20 males and 20 females, by brushing. Ten males and ten females constituting the control group were isolated in 20 l plastic containers and maintained as described for the original colony, while the other ten males and ten females were marked with correction fluid and re-introduced to the original colony. The primary purpose of the control group was to account for the fact that brushing is not effective in removing all mites from cockroaches. One week after introduction, mites from both groups of cockroaches were counted. The initial prevalence of infestation was 100% and the initial mean intensity ($\pm$SE) was 42.2 ($\pm$2.8). There was no significant difference in intensity between males and females so sexes were pooled for analysis. After one week, the marked cockroaches were recaptured. Mites were removed and counted from the control (isolated) and experimental groups and mean intensities were compared by Student's two tailed t-tests. In a subsequent experiment, mites were removed from 30 adult cockroaches, 15 males and 15 females. Cockroaches were marked as described above before being returned to the colony. After two weeks, 29 of the cockroaches were recovered (1 adult female died in the course of the experiment) and mites were counted. The mean intensity of the second experimental group was compared to that of the control group using Student's two-tailed t-tests.

To test the assertion of Schaefer and Peckham (1968) that the mites are negatively phototactic, mites were counted on the dorsal surface of 60 adult cockroaches occurring in the open under full light and compared to numbers of mites counted on the dorsal surface of 60 adult cockroaches immediately after removing egg cartons serving as cover.

Results

Population Structuring of G. schaeferi on G. portentosa

Of 1,915 cockroaches examined, 971 (50.7%) were infested with 19,421 mites exhibiting a mean intensity ($\pm$SE) of 20.0 ($\pm$0.6), with an infection intensity range of 1-116, and relative abundance ($\pm$ SE) of 10.1 ($\pm$0.4). Both prevalence and mean intensity of infestation exhibited a dramatic increase with increasing cockroach size/age. By the time cockroaches reach 40 mm the prevalence is nearly 100%. Intensity increases with cockroach length up to about 60 mm and then levels off at about 43. Mites on adult females (> 50 mm) exhibited a significantly greater intensity of infestation than on male cockroaches over 50 mm long ($t=2.67$; 493 d.f.;$p=0.008$). Eight of the nine heaviest infestations were of female cockroaches, although the infestation of penultimate intensity was of a male cockroach with 104 mites. Prevalence and intensity data of *G. schaeferi* on various size classes of *G. portentosa* are summarized in Figures 1 and 2, respectively. Raw data are provided in Appendix 1.

Overall the mite distribution among the cockroaches exhibited pronounced overdispersion, characteristic of parasite populations, with a variance-to-mean ratio (VMR) of 30.136 and *k* value of 0.182101. The standard error variance of *k* was 0.022361. The 184 most heavily infested cockroaches accounted for over half of the total mites collected; thus, more than half of the mite community was aggregated on 9.6% of the cockroaches examined.

Transmission Dynamics of G. schaeferi on G. portentosa

The initial prevalence of infestation was 100% and the initial mean intensity ($\pm$SE) was 42.2 ($\pm$2.8). There was no significant difference in intensity between males and females so sexes were pooled for analysis.

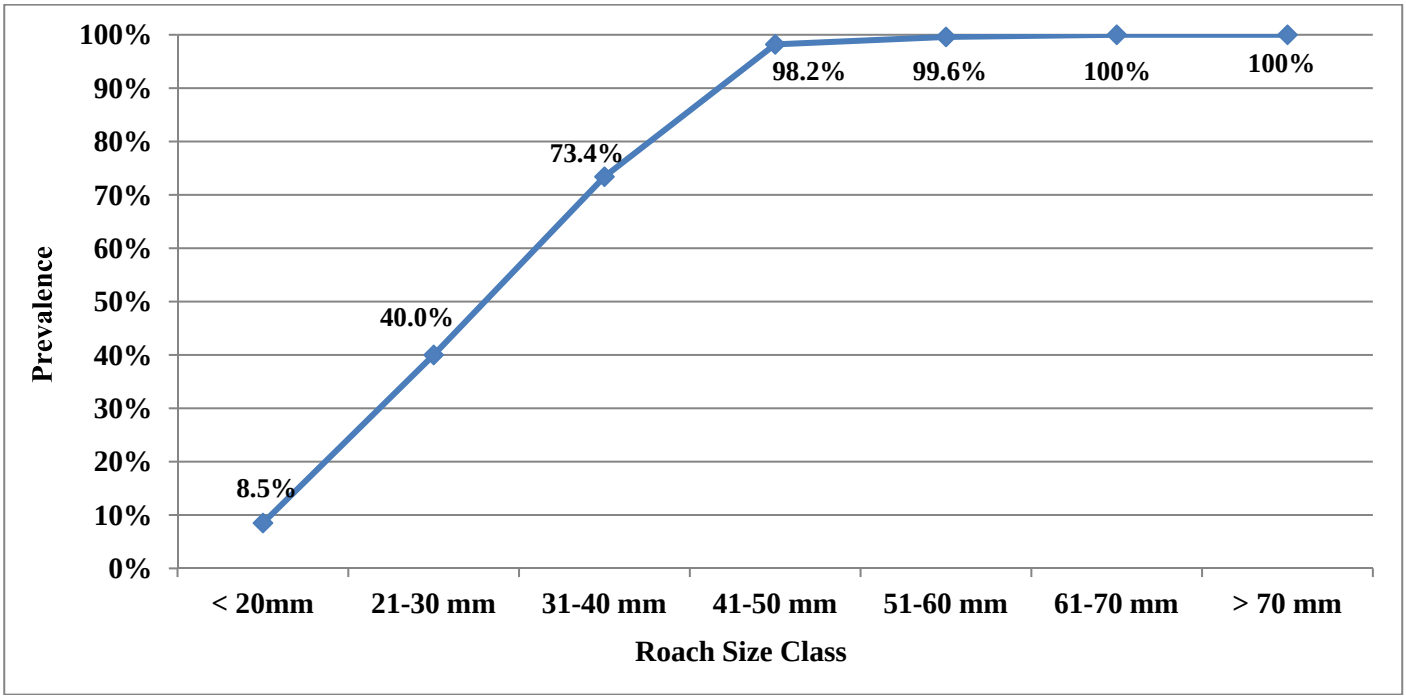

Figure 1. Prevalence of *Gromphadorholaelaps schaeferi* among various size classes of *Gromphadorhina portentosa*

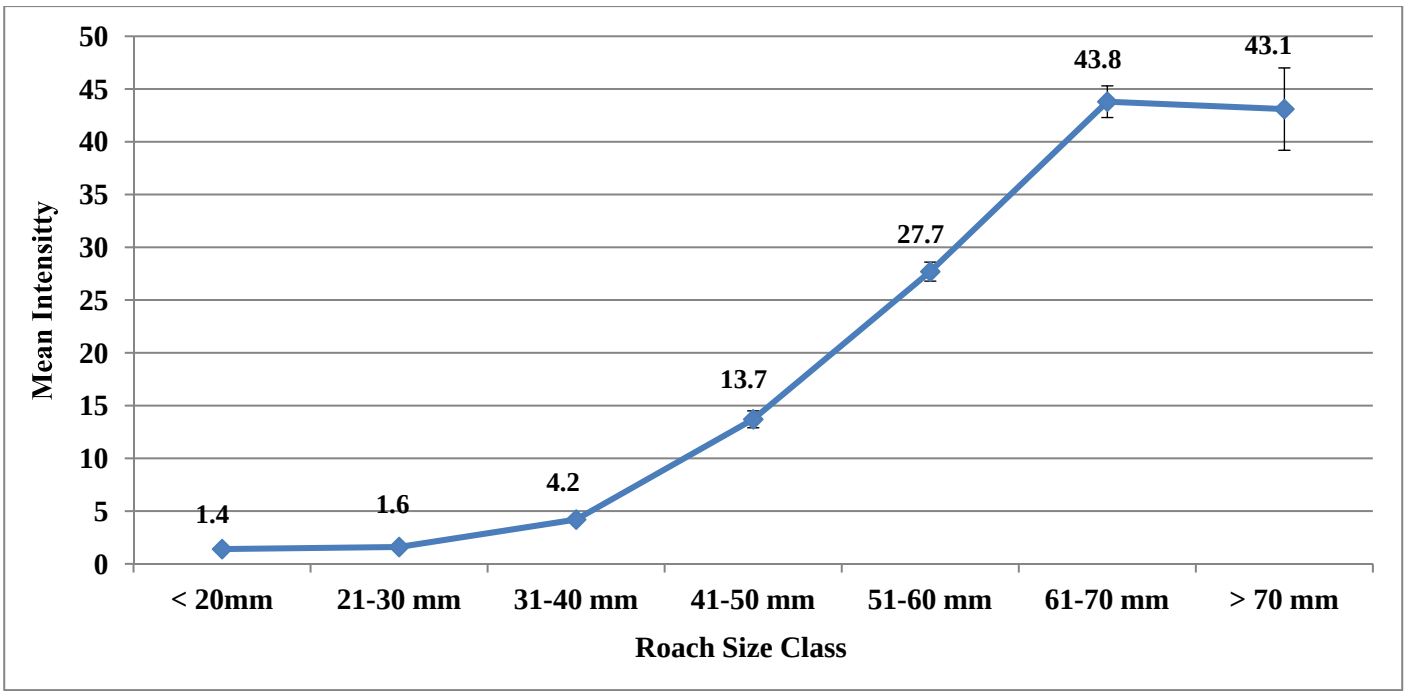

Figure 2. Mean intensity of *Gromphadorholaelaps schaeferi* among various size classes of *Gromphadorhina portentosa*. Error bars show standard error about the mean.

After one week, the prevalence of mites on the control group was 90% and the relative abundance (±SE) was 7.1 (±1.8). The prevalence on the sixteen individuals recovered from the experimental group was 100% with a mean intensity, and relative abundance, of 31.4 (±4.1). The mean number of mites on the experimental group was significantly greater than that of the control group ($t=5.85$; 34 d.f.; $p=1.0 \times 10^{-6}$). The mean number of mites of the control group was significantly less than that of initial infestation ($t=-8.29$; 58d.f.; $p=2.0 \times 10^{-11}$). A total of 142 mites were collected from the 20 roaches comprising the control group. It is assumed that most, more likely all, of these mites were residually left on the cockroaches after being brushed two weeks prior when 1,688 mites were removed from the 40 cockroaches. These data suggest that the brushing technique was effective in removing 85.6% of the mites. The mean intensity of mites of the experimental group was significantly less than that of initial infestation ($t=-2.07$; 54 d.f.; $p=0.043$). After two weeks, the prevalence of mites on the 29 individuals recovered from the experimental group was 100% with a mean intensity of 34.9 (±3.0) which was not significantly different than that of initial infestation which exhibited a mean intensity (±SE) of 40.1 (± 3.2).

Phototaxis of G. schaeferi on G. portentosa

Mites were observed on the dorsal surface of 76.7% of 60 adult cockroaches occurring in full light with a mean occurrence (±SE) of 1.6 (±0.2) and range of 0-4. This was significantly fewer than the mean (±SE) of 5.7 (±0.4) mites with a range of 0-15 occurring on the dorsal surface of 60 cockroaches immediately after the egg cartons serving as cover were removed. Mites were observed on the dorsal surface of 98.3% of adult cockroaches in the dark.

Qualitative Observations

Mites were highly vagile and negatively phototactic. Cockroaches would aggregate in large masses under egg cartons provided for cover. When the egg cartons were lifted, exposing the cockroaches, mites were commonly observed crawling about on the dorsal surface of cockroaches and were often observed on the bedding. Although mites were commonly observed on juvenile cockroaches (1st and 2nd instars), these mites were loosely associated with the cockroaches, usually moving about on the dorsal surface.

Discussion

The initial impetus for investigating the population structuring and transmission dynamics of *G. schaeferi* on *G. portentosa* was to assess the suitability of this system as an experimental model for investigating the negative binomial distribution, in which most hosts are uninfected or are only lightly infected while relatively few hosts are heavily infected/infested (Richardson et al. 2011a) by symbiotic associates. Crofton (1971) observed that such a distribution is not only characteristic of parasite populations but that the overdispersed negative binomial distribution defines parasitism. Although *G. schaeferi* exhibits an aggregated distribution evidenced by a high VMR and low *k* value, it does not conform to the "classical" negative binomial distribution as described by Bliss and Fisher (1953), which is characteristic of parasite populations (Crofton 1971). This was initially surprising in that other mite populations, symbiotic on both animals and plants, have been documented to closely conform to the negative binomial distribution (Bliss and Fisher 1953, Lanciani 1985, Hall et al., 1997). Comparison of the observed distribution of *G. schaeferi* on *G. portentosa* to the expected values of the "classical" negative binomial as described by Bliss and Fisher (1953) reveals a larger number of moderate infestations than expected and fewer heavy infestations; thus, the distribution is less heteroskedactic than expected (Fig. 3). For these reasons, it was determined that *G. schaeferi* on *G. portentosa* does not represent an ideal experimental model as defined by Richardson et al. (2011a,b) for investigation of the negative binomial. Nevertheless this system may provide a useful system for other epidemiological modeling. Raw data are provided in Table 1 to facilitate further analyses.

The variance-to-mean ratio (VMR) is a more general indicator of aggregation. Barbour and Pugliese (2000) provided an overview of application of VMR to assessment of parasite distribution as follows: A standard model in statistical ecology is to compare observed distributions with the null model of "random" distribution, typified by the Poisson distribution. For a Poisson distribution, the VMR is equal to 1. Distributions with VMRs smaller than 1 are 'under-dispersed' and those with VMRs greater than 1 are 'over-dispersed' or 'aggregated.' Thus, VMR increases as the degree of aggregation increases. The mite population on *G. portentosa* is clearly highly aggregated evidence by a VMR of 30.136.

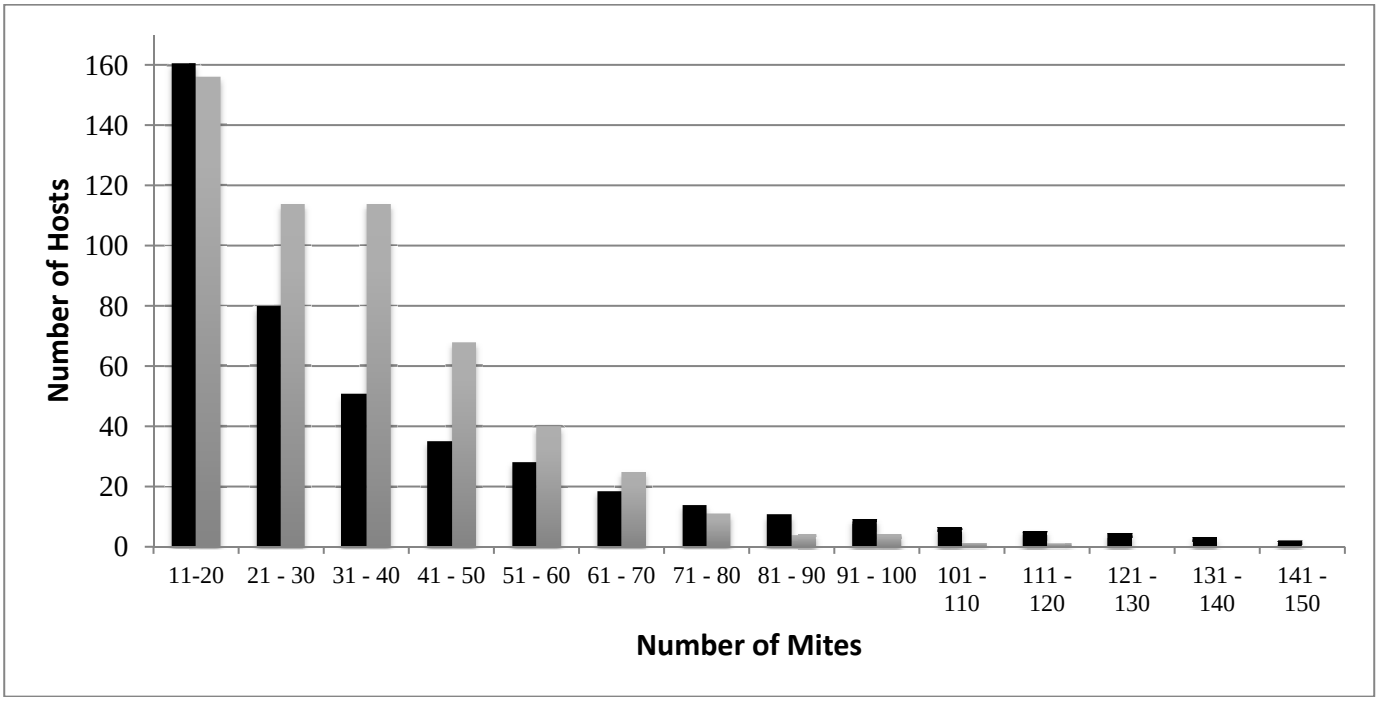

Figure 3. Frequency distribution showing expected (black bars) and observed (gray bars) values for the negative binomial applied to the distribution of mites, *Gromphadorholaelaps schaeferi* on Madagascar hissing cockroaches, *Gromphadorhina portentosa*. The display is truncated, excluding the 0 and 1-10 classes of infection.

Data presented herein collectively suggest that *G. schaeferi* exhibits low host fidelity. Although *G. schaeferi* is an obligate symbiont of *G. portentosa*, the physical association is "loose," with the mites exhibiting a high degree of vagility and pronounced movement from host to host, especially in the absence of light as the mites are negatively phototactic. Low numbers of mites observed on first and second instars suggest that these occurrences may be ephemeral and not true symbiotic associations in which the mites actually gain their sustenance from these small cockroaches. If that is the case, overdispersion and thus the negative binomial will be even less pronounced in a truncated distribution that does not take first and second instars of *G. portentosa* into account, thus diminishing the large "0" class of the overdispersed distribution. The VMR of *G. schaeferi* occurring on adult *G. portentosa* ($\geq$ 50 mm) is 10.609, which is 284% lower than the VMR of *G. schaeferi* when all size classes of cockroaches are taken into account.

Madagascar hissing cockroaches tend to aggregate in the laboratory, but in nature have been reported to form small groups consisting of about 10 individuals (Varadínova et al. 2010). Given the high prevalence and intensity of *G. schaeferi* on *G. portentosa*, in conjunction with their low degree of host fidelity and high level of vagility, it is conceivable that the small clusters of individuals in nature as reported by Varadínova et al. (2010) represent relatively homogenous and well-defined patches of distribution for *G. schaeferi*. Thus, the negative binomial distribution may be realized among interacting clusters of *G. portentosa* in nature with these small infra-populations of hosts, in contrast to infested individuals, serving as the interacting units of infestation. This seems a reasonable possibility in the instance of a symbiont with high vagility and low host fidelity on a host characterized by high levels of aggregation that would maximize horizontal transmission. In such a scenario, the small groups, or infrapopulations of cockroaches would be analogous to individual apple leaves infested with red mites as Bliss and Fisher (1953) used to typify the negative binomial distribution.

Bell et al. (2007) stated that "it is difficult to conceive of any group of animals that are as universally and diversely social as cockroaches….and are thus potentially excellent models with which to test general hypotheses in social ecology." Laboratory studies confirm that *G. portentosa* and other Madagascar hissing cockroaches are social insects evidenced by gregariousness (Yoder and Grojean 1997), a relatively high degree of maternal care (Roth

and Willis 1960, Schaefer and Peckham 1968, Perry and Nalepa 2003, Bell et al. 2007), male-male competition with establishment of hierarchical dominance ranking (Clark and Moore 1994, Clark 1998), mate selection based on female discrimination (Clark and Moore 1995a), discrimination between sexes and among social classes on basis of olfactory cues (Leibensperger et al. 1985), and complex acoustic communication (Nelson and Fraser 1980, Fraser and Nelson 1982, 1984, Clark and Moore 1995 a,b,c, Clark 1998, Sueur and Aubin 2006). If indeed hissing cockroaches exhibit a high level of sociality in nature, a suite of complicating factors arise that affect population structuring of symbionts among host individuals, both within the "colony" (Royce and Rossignol 1990, Pie et al. 2004) and among "colonies" or populations (Schmid-Hempel 1998). Such complexities can lead to situations where the 'type' of overdispersion is difficult to specify on biological grounds (Schmid-Hempel 1998, Lindén and Mäntyniemi 2011). Disease transmission among social insects exhibits different dynamics with clusters of individuals, or colonies, playing a role analogous to individuals in populations of solitary-living individuals. This may explain why *G. schaeferi* on *G. portentosa* does not conform to the "classical" negative binomial distribution of Bliss and Fisher (1953) that is characteristic of parasite populations (Crofton, 1971). Whiteman and Parker (2004) pointed out that variations in parasite responses to host sociality may yield misleading results and incorrect interpretations concerning dynamics of aggregation comprising parasite population structuring. Whiteman and Parker (2004) concluded that host-parasite interactions only make sense in the context of basic life-history characteristics of each participant. Until the biology of *G. schaeferi* and *G. portentosa* is further elucidated, a detailed explanation of the ecological dynamics underlying the population structuring of *G. schaeferi* on *G. portentosa* will remain a matter of speculation. As pointed out by Lindén and Mäntyniemi (2011), at least mean-variance relationships can, in all considerations, be described appropriately. Until a better understanding of the population structuring and dynamics of *G. portentosa* is realized, the VMR should be the primary means utilized to assess overdispersion among symbionts of Madagascar hissing cockroaches.

Schmid-Hempel (1998) proposed a "macroscopic" view in assessing disease transmission among populations of social insects in which colonies take the place of individuals within a population and are regarded as epizootiological units. Given the ease with which large numbers of individuals may be raised in the laboratory, along with the ease of manipulation of the cockroaches and mites, *G. schaeferi* on *G. portentosa* may offer a valuable epizootiological model for investigating the transmission of diseases among social organisms once the natural history of this system is better defined. This model may prove valuable as a laboratory tool to assess theoretical epidemiological models for disease transmission among social organisms, from honeybees to humans. Field studies investigating the natural history of *G. portentosa* are warranted to facilitate further investigation of these and other hypotheses.

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Table 1. Raw data for distribution of the mite *Gromphadorholaelaps schaeferi* on the Madagascar hissing cockroach *Gromphadorhina portentosa* showing number of observations (n), length of roach (mm), sex for roaches ≥ 50mm (M=male; F=female), and number of mites.

n	Length (mm)	Sex	# mites		n	Length (mm)	Sex	# mites		n	Length (mm)	Sex	# mites		n	Length (mm)	Sex	# mites
19	9	-	0		3	26	-	2		1	36	-	9		1	42	-	11
84	10	-	0		1	26	-	5		1	36	-	15		2	42	-	15
2	10	-	1		11	27	-	1		3	37	-	0		1	42	-	17
143	11	-	0		1	27	-	2		2	37	-	1		1	42	-	18
3	26	-	2		8	28	-	1		3	37	-	2		1	42	-	21
1	26	-	5		6	28	-	2		2	37	-	3		1	42	-	24
11	27	-	1		1	28	-	3		1	37	-	4		1	43	-	0
1	27	-	2		9	29	-	1		3	37	-	5		2	43	-	1
8	28	-	1		5	29	-	2		1	37	-	9		1	43	-	3
6	28	-	2		5	29	-	3		1	37	-	10		1	43	-	4
1	28	-	3		13	30	-	1		1	37	-	19		1	43	-	5
9	29	-	1		4	30	-	2		2	38	-	0		1	43	-	6
5	29	-	2		1	30	-	4		2	38	-	1		3	43	-	7
5	29	-	3		2	30	-	5		2	38	-	2		3	43	-	10
13	30	-	1		1	30	-	9		3	38	-	3		1	43	-	11
4	30	-	2		13	31	-	0		2	38	-	4		1	43	-	13
1	30	-	4		1	31	-	1		3	38	-	5		1	43	-	18
2	30	-	5		1	31	-	2		2	39	-	0		1	43	-	19
1	30	-	9		1	31	-	4		3	39	-	1		2	44	-	1
13	31	-	0		1	31	-	9		3	39	-	2		1	44	-	2
1	31	-	1		10	32	-	0		5	39	-	3		1	44	-	4
1	31	-	2		4	32	-	1		2	39	-	5		1	44	-	7
1	31	-	4		9	32	-	2		2	39	-	6		2	44	-	8
1	31	-	9		3	32	-	3		1	39	-	8		1	44	-	9
10	32	-	0		1	32	-	4		1	39	-	9		1	44	-	11
4	32	-	1		1	32	-	5		1	39	-	11		1	44	-	12
9	32	-	2		1	32	-	7		1	39	-	15		1	44	-	13
3	32	-	3		5	33	-	0		1	40	-	0		1	44	-	14
1	32	-	4		4	33	-	1		1	40	-	1		1	45	-	3
1	32	-	5		1	33	-	2		1	40	-	3		1	45	-	6
1	32	-	7		1	33	-	3		2	40	-	4		1	45	-	7
5	33	-	0		1	33	-	4		1	40	-	5		1	45	-	9
4	33	-	1		2	33	-	5		1	40	-	6		2	45	-	11
1	33	-	2		1	33	-	6		2	40	-	7		1	45	-	12
1	33	-	3		1	33	-	14		1	40	-	8		1	45	-	13
1	33	-	4		2	34	-	0		2	40	-	10		1	45	-	16
2	33	-	5		3	34	-	1		1	40	-	12		1	45	-	22
1	33	-	6		3	34	-	2		1	40	-	22		2	45	-	26

Table 1. *Continued.*

n	Length (mm)	Sex	# mites		n	Length (mm)	Sex	# mites		n	Length (mm)	Sex	# mites		n	Length (mm)	Sex	# mites
1	34	-	9		2	35	-	2		1	41	-	12		4	46	-	9
1	34	-	10		1	35	-	3		1	42	-	1		3	46	-	10
8	35	-	0		3	35	-	4		2	42	-	2		1	46	-	11
6	35	-	1		1	35	-	5		1	42	-	5		2	46	-	12
2	35	-	2		1	35	-	8		2	42	-	6		1	46	-	13
1	35	-	3		5	36	-	0		1	42	-	8		1	46	-	15
3	35	-	4		7	36	-	1		2	42	-	9		2	46	-	16
1	35	-	5		4	36	-	2		1	42	-	10		1	46	-	18
1	24	-	3		4	36	-	3		1	41	-	12		1	46	-	22
10	25	-	1		2	36	-	4		1	42	-	1		1	46	-	24
4	25	-	2		1	36	-	7		2	42	-	2		1	47	-	2
11	26	-	1		1	36	-	8		1	42	-	5		1	47	-	6
1	47	-	10		2	51	F	17		1	54	F	18		1	56	M	34
1	47	-	11		2	51	M	7		2	54	F	21		2	56	M	37
1	47	-	14		1	51	M	9		2	54	F	22		1	56	M	40
1	47	-	15		1	51	M	12		2	54	F	30		1	56	M	47
1	47	-	19		1	51	M	17		1	54	M	7		1	56	M	50
1	47	-	20		1	51	M	19		1	54	M	9		1	56	M	51
1	47	-	21		1	51	M	23		1	54	M	10		1	57	F	9
1	47	-	23		1	51	M	26		1	54	M	11		1	57	F	15
1	47	-	24		1	51	M	29		2	54	M	15		1	57	F	22
1	47	-	29		1	51	M	32		1	54	M	17		1	57	F	29
1	47	-	35		1	51	M	34		2	54	M	18		1	57	F	31
1	47	-	42		1	51	M	37		1	54	M	19		1	57	F	32
1	48	-	4		1	51	M	40		1	54	M	20		1	57	F	35
1	48	-	5		1	51	M	50		1	54	M	24		1	57	F	51
1	48	-	8		1	52	F	7		1	54	M	26		1	57	F	64
3	48	-	9		1	52	F	8		1	54	M	27		1	57	M	6
1	48	-	11		1	52	F	12		1	54	M	28		4	57	M	13
3	48	-	15		1	52	F	22		1	54	M	31		1	57	M	16
1	48	-	16		1	52	F	30		1	54	M	32		1	57	M	19
1	48	-	17		1	52	-	71		1	54	M	33		1	57	M	20
1	48	-	18		1	52	M	4		1	54	M	35		1	57	M	21
1	48	-	20		1	52	M	9		1	54	M	36		1	57	M	22
1	48	-	24		1	52	M	20		1	54	M	56		2	57	M	23
2	48	-	28		1	52	M	23		1	55	F	3		1	57	M	24
1	48	-	34		1	52	M	24		1	55	F	10		2	57	M	27
1	49	-	4		2	52	M	27		1	55	F	15		1	57	M	28
1	49	-	6		2	52	M	28		1	55	F	20		1	57	M	32
1	49	-	9		1	52	M	29		1	55	M	4		1	57	M	35
3	49	-	10		2	52	M	34		1	55	M	7		1	57	M	36
2	49	-	11		1	52	M	46		1	55	M	10		1	57	M	37
1	49	-	12		1	53	F	4		1	55	M	11		3	57	M	38
1	49	-	13		1	53	F	14		1	55	M	12		1	57	M	42
1	49	-	14		1	53	F	16		1	55	M	13		1	57	M	43
1	49	-	17		1	53	F	17		2	55	M	14		1	57	M	48
1	49	-	18		1	53	F	19		1	55	M	24		1	57	M	55
1	49	-	22		1	53	F	33		2	55	M	25		1	57	M	60
1	49	-	32		1	53	F	42		1	55	M	26		1	58	F	5
1	49	-	34		1	53	M	2		1	55	M	32		1	58	F	7
1	49	-	49		1	53	M	13		2	55	M	33		1	58	F	18
1	49	-	50		1	53	M	14		1	55	M	36		2	58	F	21
1	50	F	8		1	53	M	15		1	55	M	38		1	58	F	22
2	50	F	12		3	53	M	16		1	55	M	39		1	58	F	26
1	50	F	14		1	53	M	17		1	55	M	41		1	58	F	30
1	50	F	20		1	53	M	18		1	55	M	45		2	58	F	45
1	50	F	56		1	53	M	19		1	55	M	46		1	58	M	10
1	50	M	9		1	53	M	20		1	55	M	47		1	58	M	14
2	50	M	12		2	53	M	21		1	55	M	48		1	58	M	15

Table 1. *Continued.*

n	Length (mm)	Sex	# mites		n	Length (mm)	Sex	# mites		n	Length (mm)	Sex	# mites		n	Length (mm)	Sex	# mites
1	50	M	17		1	53	M	22		1	56	M	6		1	58	M	17
2	50	M	19		2	53	M	23		1	56	M	11		1	58	M	20
1	50	M	21		1	53	M	25		1	56	M	29		1	58	M	21
1	50	M	25		2	53	M	27		1	56	M	40		1	58	M	23
1	50	M	31		1	53	M	28		1	56	M	11		1	58	M	27
1	50	M	35		1	53	M	31		1	56	M	13		1	58	M	31
1	50	M	43		1	53	M	45		1	56	M	14		3	58	M	34
1	50	M	45		1	53	M	53		1	56	M	15		2	58	M	38
1	51	F	0		1	53	M	55		2	56	M	16		2	58	M	40
1	51	F	2		1	53	M	66		1	56	M	20		1	58	M	50
1	51	F	7		1	54	F	12		1	56	M	26		1	58	M	61
1	51	F	12		1	54	F	15		1	56	M	30		1	59	F	11
1	59	F	18		1	61	M	9		1	63	M	43		1	67	F	47
2	59	F	20		1	61	M	12		1	63	M	45		1	67	F	57
1	59	F	26		1	61	M	15		1	63	M	50		1	67	F	77
1	59	F	33		1	61	M	16		1	63	M	51		1	67	M	5
1	59	F	36		1	61	M	20		1	63	M	58		1	67	M	17
1	59	F	56		1	61	M	30		2	63	M	62		1	67	M	41
1	59	F	63		3	61	M	32		1	64	F	14		1	68	F	15
1	59	M	3		1	61	M	39		1	64	F	29		1	68	F	30
1	59	M	12		1	61	M	40		1	64	F	32		1	68	F	32
1	59	M	16		1	61	M	41		1	64	F	34		1	68	F	35
1	59	M	19		1	61	M	43		1	64	F	35		1	68	F	44
1	59	M	22		1	61	M	47		1	64	F	39		1	68	F	46
1	59	M	23		2	61	M	59		1	64	F	40		1	68	F	48
1	59	M	24		1	61	M	63		1	64	F	49		1	68	F	59
1	59	M	26		1	61	M	65		1	64	F	58		1	68	F	63
2	59	M	30		1	61	M	75		1	64	F	69		1	68	F	74
2	59	M	32		1	61	M	78		1	64	F	91		1	68	F	86
2	59	M	35		1	62	F	16		1	64	M	4		1	68	M	37
2	59	M	39		1	62	F	24		2	64	M	32		1	68	M	44
1	59	M	49		1	62	F	28		1	64	M	35		1	69	F	27
1	59	M	54		1	62	F	34		1	64	M	37		1	69	F	35
1	59	M	55		1	62	F	36		1	64	M	43		1	69	F	37
1	59	M	56		1	62	F	37		1	64	M	62		1	69	F	41
1	59	M	57		1	62	F	38		1	64	M	66		1	69	F	43
1	59	M	61		1	62	F	47		1	64	M	69		1	69	F	45
1	59	M	65		1	62	F	57		1	65	F	12		2	69	F	47
1	59	M	67		1	62	F	58		1	65	F	17		1	69	F	51
1	59	M	68		1	62	M	25		1	65	F	31		1	69	F	53
1	59	M	81		1	62	M	27		1	65	F	35		1	69	M	42
1	60	F	8		2	62	M	28		1	65	F	41		1	69	M	72
1	60	F	14		2	62	M	35		2	65	F	47		1	70	F	10
1	60	F	16		2	62	M	40		1	65	F	63		1	70	F	38
1	60	F	18		1	62	M	41		1	65	F	66		1	70	F	46
1	60	F	23		1	62	M	47		1	65	F	85		1	70	F	50
1	60	F	27		1	62	M	51		1	65	M	14		1	70	F	54
1	60	F	32		1	62	M	55		1	65	M	67		1	70	F	56
1	60	F	41		1	62	M	67		1	65	M	79		1	70	F	71
1	60	F	42		1	62	M	70		1	65	M	104		1	70	M	58
1	60	F	47		1	63	F	16		1	66	F	18		1	71	F	14
1	60	F	48		1	63	F	26		1	66	F	27		1	71	F	28
1	60	F	56		1	63	F	27		1	66	F	29		1	71	F	29
1	60	F	67		1	63	F	28		1	66	F	35		1	71	F	56
1	60	M	8		2	63	F	31		2	66	F	40		1	71	M	9
1	60	M	11		1	63	F	41		1	66	F	41		1	71	M	34
1	60	M	20		1	63	F	55		1	66	F	46		1	72	F	37
1	60	M	24		1	63	F	61		1	66	F	65		1	72	F	50
2	60	M	25		1	63	F	92		1	66	F	96		2	72	F	57

Table 1. *Continued.*

n	Length (mm)	Sex	# mites		n	Length (mm)	Sex	# mites		n	Length (mm)	Sex	# mites		n	Length (mm)	Sex	# mites
1	60	M	27		1	63	M	6		1	66	F	116		1	72	F	71
1	60	M	29		1	63	M	11		1	66	M	21		1	72	F	84
2	60	M	32		1	63	M	14		1	66	M	32		1	72	M	20
1	60	M	34		1	63	M	15		1	66	M	36		1	72	M	23
1	60	M	35		1	63	M	20		1	66	M	56		1	72	M	44
2	60	M	36		1	63	M	22		1	66	M	76		1	72	M	71
1	60	M	44		1	63	M	32		1	67	F	14		1	73	F	99
1	61	F	26		1	63	M	33		1	67	F	24		1	74	F	30
1	61	F	30		1	63	M	34		1	67	F	30		1	74	F	54
2	61	F	50		1	63	M	38		1	67	F	40		1	75	F	34
1	61	F	53		2	63	M	39		1	67	F	41		1	75	F	42
1	61	F	58		1	63	M	41		1	67	F	44		2	76	F	29
1	76	F	39															
1	76	F	42															
1	76	F	59															
1	76	M	20															
1	77	F	57															
1	78	F	33															
1	85	M	27															